5

Apterygote Hexapods

1. Introduction

Traditionally, the groups included in the term "apterygote hexapods," namely, the Collembola, Protura, Diplura, and Thysanura (including Microcoryphia and Zygentoma), were considered orders of primitively wingless insects and placed in the subclass Apterygota (Ametabola). They show the following common features: lack of wings, lack of a pleural sulcus on the thoracic segments, presence of pregenital abdominal appendages, slight or absent metamorphosis, and indirect sperm transfer. As more information on their structure and habits has become available, it has become apparent that (1) their status as insects (except for Thysanura) is doubtful and (2) the relationship of the groups with each other is more distant than originally believed. Several authors have therefore recommended that the insectan subclass Apterygota be reserved solely for the Thysanura and that the Collembola, Protura, and Diplura each be given the rank of class, with the Collembola and Protura considered as sister groups within the Ellipura (see Figure 1.11). These three groups differ fundamentally from insects in several features; for example, they are entognathous, have intrinsic musculature in the antennae, and lack compound eyes which are characteristic of most insects, at least in the adult stage. Thus, the Ellipura and Diplura are sometimes considered sister groups within the Entognatha. However, other analyses indicate that the Entognatha is a paraphyletic assemblage (see Chapter 1, Section 3.3.1).

The Collembola are probably furthest removed from the winged insects. They possess only six abdominal segments, a postantennal sensory organ similar to the organ of Tömösvary found in myriapods, gonads with lateral (rather than apical) germaria, and eggs in which there is total cleavage. Non-insectan features of the Protura are the absence of antennae (perhaps a secondary condition associated with their soil-dwelling habit), the occurrence of anamorphosis, and a genital aperture that opens behind the 11th segment. Diplura are superficially similar to Thysanura, with which some authors group them. However, in addition to the features mentioned above, they differ from typical insects in having unusual respiratory and reproductive systems. Even though all Thysanura are considered insectan, it is now apparent that the group contains two distinct subgroups, the Microcoryphia and the Zygentoma (= Thysanura *sensu stricto*), to which some authors accord ordinal status. The primary basis for this distinction concerns the mouthparts. In the Microcoryphia (such as *Machilis* and its allies, the bristletails) the mandibles have a single articulation with

the head and bite with a rolling motion. In the Zygentoma (which includes silverfish and firebrats), on the other hand, there is a dicondylic articulation of the mandible, which thus bites transversely as in pterygote insects. As noted in Chapter 1, differences in the structure and operation of the mouthparts are of fundamental phylogenetic importance.

2. Collembola

SYNONYMS: Oligentoma, Oligoentomata COMMON NAME: springtails

Small to minute wingless hexapods; head pro- or hypognathous, antennae segmented, compound eyes absent, mouthparts entognathous; abdomen 6-segmented, typically with three medially situated pregenital appendages (collophore on segment 1, retinaculum on segment 2, furcula on segment 4), gonopore on 5th segment.

Collembola are abundant on every continent, including Antarctica. About 6500 species have been described, including more than 1600 from Australia, 300 from the United Kingdom, and about 840 from North America. Individual species may be quite cosmopolitan, sometimes as a result of human activity when they may become pests.

Structure

Collembola vary in length from about 0.2 to 10 mm. They are generally dark, but many species are whitish, green, or yellowish, and some are striped or mottled. The body is either elongate (Arthropleona) (Figure 5.1B) or more or less globular (Symphypleona and Neelipleona) (Figure 5.1A). The head is primitively prognathous, but is hypognathous

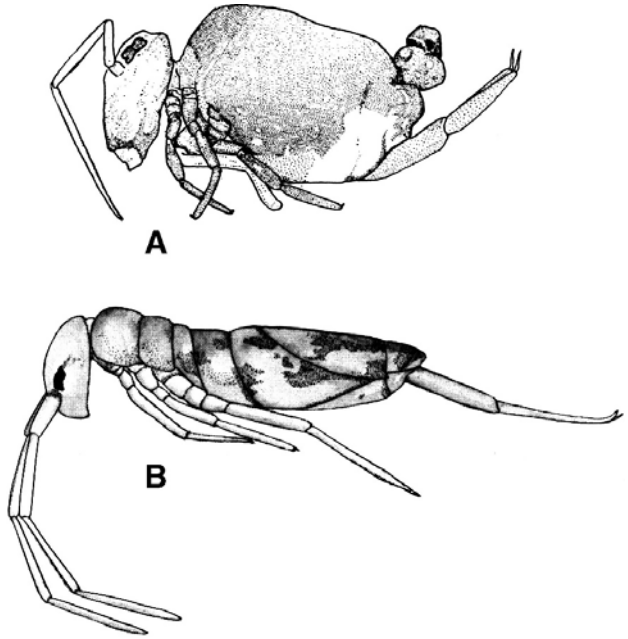

FIGURE 5.1. Collembola. (A) *Sminthurus purpurescens* (Sminthuridae); and (B) *Entomobrya nivalis* (Entomobryidae). [Reprinted from Elliott A. Maynard, 1951, *A Monograph of the Collembola or Springtail Insects of New York State*, Comstock Publishing Co., Inc.]

in the Symphypleona and Neelipleona, and the mouthparts are enclosed within a pouch formed by the ventrolateral extension of the head capsule. The mouthparts are typically of the chewing type, though in many species they are rasping or suctorial. The 4-segmented antennae vary greatly in length and each segment may be subdivided into two (segments 1 and 2) or numerous (segments 3 and 4) subsegments. Immediately behind the antennae is a structure of varied form, the postantennal organ, which appears to have an olfactory function. Compound eyes never occur, but a varied number of ocelli (up to eight) are found on each side of the head. The thoracic segments are distinct in Arthropleona, but not in Symphypleona and Neelipleona; in all species the prothorax is small or vestigial. In the Symphypleona and Neelipleona the thorax is fused with the abdomen and individual segments are not easily distinguished except at the posterior end. The legs have no true tarsus but terminate in one or two claws that arise from the tibia. No more than six abdominal segments can be distinguished at any time (even during embryonic development). The first abdominal segment bears the collophore (ventral tube), which arises by fusion and differentiation of the embryonic appendages. The tube contains a pair of vesicles that can be extruded by hemolymph pressure. The tube appears to have several functions, though it was originally named because it was thought to be adhesive (Greek *colle*, glue). Other likely functions include gaseous exchange and, especially, salt-water balance. Most Collembola have a springing organ (furcula) on the fourth abdominal segment, held under tension beneath the body by a hooklike structure, the retinaculum, formed from the appendages of the third abdominal segment. When released from the retinaculum, the furcula is forced downward and backward by both muscular action and hemolymph pressure. As it strikes the substrate, the animal is thrown through the air, sometimes a significant distance (e.g., up to 30 cm in some sminthurids). Abdominal appendages may be greatly reduced in small subterranean forms. Cerci are absent in Collembola. Some species are ecomorphic, their form changing from instar to instar as a result of unusual environmental conditions, others are cyclomorphic (having seasonally different forms and habits, usually in summer and winter), and some show epitoky in which reproductive instars are morphologically different from non-reproductive (feeding instars) with which they alternate.

Noteworthy features of the internal structure of Collembola are the absence of Malpighian tubules and, in most species, tracheal system. However, a pair of spiracles between the head and thorax, leading to tracheae in the head, sometimes also the body, have been reported for a few Symphypleona. The nervous system is specialized and includes brain, subesophageal ganglion, and three ventral ganglia, the ganglia of the abdominal segments having fused with the metathoracic ganglion.

Life History and Habits

Springtails are almost ubiquitous, being found in high latitudes (e.g., 84° south in Antarctica) and altitudes (above 7700 m in the Himalayas), deserts, and glaciers, in addition to more conventional biomes. Within these regions they occupy a wide range of habitats, though they are most abundant and diverse in moist soil, leaf litter, and rotting wood. Others live in dung, in the fleshy parts of fungi, in the nests of termites, ants, and vertebrates, on grasses, and in flowers. Several species occur in caves, on the surface of standing water (including, rarely, tidal pools), and in both marine and freshwater intertidal zones, though very few are truly aquatic. Occasionally, species form large aggregations on the surface of snow, though the significance of this is not clear. Most Collembola cannot tolerate desiccation, and those that colonize dry habitats show various morphological, physiological,

and behavioral adaptations, such as scales or hairs, specific desiccation-resistant stages (including more or less completely dried out "anhydrobiotic" forms), and activity restricted to periods when the relative humidity is high. Collembola are saprophagous, fungivorous (including some spore feeders), or phytophagous (including some pollen feeders), and some species appear to have an intrinsic gut cellulase. Only rarely are they predaceous. Though a few species are occasionally of economic importance because of the damage they cause to plants, overall Collembola may be considered beneficial. By feeding on fungal hyphae and decaying material, they may influence mycorrhizal growth and control fungal diseases (Hopkin, 1997).

In adult Collembola reproductive and feeding instars alternate. Most species of Collembola reproduce sexually though a few soil-dwelling species are parthenogenetic. Sperm transfer is usually indirect, males placing their stalked spermatophores on the substrate, to be found by females as a result of aggregation (perhaps involving pheromones) or after an elaborate courtship dance in which the male grasps the female using spines on his antennae, head, or legs, and draws her over the spermatophore. The pale, spherical eggs are laid singly or in small clusters (sometimes several females oviposit collectively) and may be covered with freshly eaten soil and fecal material, or cleaned by the adults, to prevent fungal infection. There is little change in external form as the young animal develops, and sexual maturity is reached usually after 5–10 molts. As many as 50 molts may occur during the adult phase.

Phylogeny and Classification

According to Kukalová-Peck (1991), the early Collembola were semiaquatic. The earliest fossil collembolan, *Rhyniella praecursor*, from the Lower Devonian of Scotland resembled modern isotomids. Other fossils are known from the Lower Permian of South Africa, the Upper Cretaceous of Canada, and Tertiary amber deposits, the latter being assignable to extant genera. Currently, the two most primitive families are thought to be the Hypogastruridae and Isotomidae, with the Entomobryidae and Sminthuridae among the most advanced. Early classifications [e.g., that of Gisin (1960)] arranged extant species of the order Collembola in two suborders, Arthropleona and Symphypleona, principally on the basis of the striking difference in body form, and five families. Nowadays, up to 14 families are recognized, and these are allocated among three orders within the class Collembola, the round-bodied Neelidae being separated from the Arthropleona in their own order Neelipleona. However, lack of information prevents the construction of a phylogenetic tree. Of the extant families, the largest and most common are the Hypogastruridae, Neanuridae, Onychiuridae, Entomobryidae, Isotomidae, and Sminthuridae.

Order Arthropleona

Superfamily Poduroidea

The HYPOGASTRURIDAE (580 species) are generally 1–3 mm in length, whitish, pinkish, or darkly colored Collembola with a predominantly holarctic distribution. They have an obvious prothorax, a granular cuticle, and short antennae, but a postantennal organ may or may not be present. They are found in a wide range of habitats though most species live among decaying vegetation, in soil, in cracks in the bark of trees, or in fungi. Some hypogastrurids are known as "snow fleas" through their being found, sometimes in immense

numbers, jumping about on snow, usually shortly after a period of mild weather. One widely distributed form, *Hypogastrura (Ceratophysella) denticulata* (likely a complex of several species), sometimes becomes a pest in mushroom cellars.

The majority of NEANURIDAE (1160 species) are found under stones and bark, or in soil and leaf litter where they feed on fungal hyphae that they pierce with their sharp mouthparts. Other species, however, are predaceous, eating rotifers, other Collembola, and their eggs. ONYCHIURIDAE (600 species) are soil- and litter-dwelling collembolans that lack ocelli and a furcula.

Superfamily Entomobryoidea

The characteristics of the ISOTOMIDAE (over 1000 species) are highly varied, and future work may well result in its being subdivided into several additional families. Isotomids are found worldwide, in a range of biomes, including the polar regions, arid areas, and seashores, though many are conventional inhabitants of soil or leaf litter. Many species, especially the soil dwellers, are cosmopolitan. The family ENTOMOBRYIDAE (Figure 5.1B), with 1365 species, includes many of the larger Collembola that reach 5 mm or more in length. Species have a greatly reduced prothorax and a smooth cuticle; a postantennal organ may or may not be present. They may be found in soil or leaf litter, under bark, in moss, and on vegetation. Some species are naturally cosmopolitan, and others have been transferred around the world by human activity.

Order Neelipleona

The approximately 25 species in this order are included in a single family NEELIDAE. These tiny collembolans (0.5 mm or less long) live in soil and leaf litter. They differ from Symphypleona in that their rounded body is formed from expansion of thoracic rather than abdominal segments.

Order Symphypleona

Superfamily Sminthuroidea

Most of the 890 species of SMINTHURIDAE (Figure 5.1A) are 1–3 mm in length and have a roundish body, hypognathous head, and conspicuous ocelli. A postantennal organ is absent. Often there is sexual dimorphism, with the antennae of males having hooks and spines. Most sminthurids are epigaeic, living near the surface of leaf litter, or on grasses or other low-growing vegetation. A number of species are economically important. For example, *Sminthurus viridis*, the lucerne flea, a European species introduced into Australia, has become an important pest on alfalfa (lucerne) and other leguminous crops. Other species may do considerable damage in greenhouses and to many garden vegetables at the seedling stage.

Literature

Accounts of the biology of Collembola are provided by Fjellberg (1985), Greenslade (1991, 1994), Hopkin (1997), and Christiansen and Bellinger (1998). Keys for their identification are to be found in Christiansen and Bellinger (1998) [North American species], Gisin (1960) [European species] (in German), and Greenslade (1991) [Australian families].

Christiansen, K., and Bellinger, P., 1998, *The Collembola of North America North of the Rio Grande*, 2nd ed., Grinnell College, Grinnell, IA.

Fjellberg, A., 1985, Recent advances and future needs in the study of Collembola biology and systematics, *Quaest. Entomol.* **21**:559–570.

Gisin, H., 1960, *Collembolenfauna Europas*, Museum d'histoire naturelle, Geneva.

Greenslade, P., 1994, Collembola, in: *Zoological Catalogue of Australia*, Vol. 22 (W. W. K. Houston, ed.), CSIRO, Melbourne.

Greenslade, P. J., 1991, Collembola, in: *The Insects of Australia*, 2nd ed., Vol. I (CSIRO, ed.), Melbourne University Press, Carlton, Victoria.

Hopkin, S. P., 1997, *Biology of the Springtails (Insecta: Collembola)*, Oxford University Press, Oxford.

Kukalová-Peck, J., 1991, Fossil history and the evolution of hexapod structures, in: *The Insects of Australia*, 2nd ed., Vol. I (CSIRO, ed.), Melbourne University Press, Carlton, Victoria.

3. Protura

SYNONYM: Myrientomata COMMON NAME: proturans

Minute wingless hexapods; head cone-shaped, compound eyes, ocelli, and antennae absent, mouthparts entognathous and suctorial; foreleg modified as a sense organ; abdomen 12-segmented in adult with appendages on first three segments; gonopore (two in males) behind 11th segment; cerci absent.

About 660 species of proturans have been described worldwide. Of these, about 80 are European (including 20 in Britain), 30 Australian, and about 20 North American, though the latter figure may be misleading, reflecting the lack of taxonomic work done on this group.

Structure

Proturans (Figure 5.2) are elongate, generally pale arthropods 2 mm or less in length. The head is cone-shaped and bears anteriorly the styliform entognathous mouthparts. Photoreceptor organs are absent from the head, as are typical antennae. However, a pair of "pseudoculi" occur dorsolaterally that may be humidity receptors or chemosensory. The thoracic segments are distinct, though the first is greatly reduced. The six identical legs have an unsegmented tarsus. The forelegs are generally not used in locomotion but are held aloft

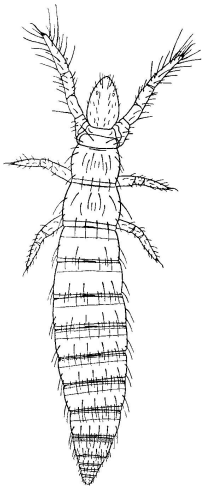

FIGURE 5.2. *Acerella barberi*, a proturan. [From H. E. Ewing, 1940, The Protura of North America, *Ann. Entomol. Soc. Am.* **33**:495–551. By permission of the Entomological Society of America.]

and probably act as sense organs. In adult proturans the abdomen is 12-segmented; in the newly hatched animal there are only 9 abdominal segments, 3 being added anamorphically during postembryonic development. Short, unsegmented or 2-segmented appendages with eversible vesicles are found on the first three abdominal segments. Cerci are absent.

Internally there are no distinct Malpighian tubules, but six papillae occur at the junction of the midgut and hindgut, and these may serve an excretory function. A tracheal system is present in Eosentomoidea, originating from paired meso- and metatergal spiracles, but not in other groups. The tracheae do not anastomose. The nervous system is generalized, with discrete ganglia in the first seven abdominal segments.

Life History and Habits

Like springtails, proturans are found in a variety of moist habitats. Although frequently overlooked because of their small size, they are quite numerous in certain situations particularly in soil and litter. Few details of their biology are available. They are thought to be fungivorous. It is reported that four juvenile stages are passed through before sexual maturity is reached (five in male Acerentomidae which have a preimago instar), but it is not known whether proturans molt when adult. There are probably several generations per year with, in cooler climates, the adults spending the winter in a dormant condition.

Phylogeny and Classification

Tuxen (1964) recognized two suborders and three families within the class and order Protura, namely, the Eosentomoidea (family EOSENTOMIDAE) and Acerentomoidea (families ACERENTOMIDAE and PROTENTOMIDAE). However, following the description of *Sinentomon erythranum* by Yin (1965), which shows morphological features of all three families and may be the most primitive living proturan, some authors (e.g., Nosek, 1973) have placed this species in its own suborder Sinentomoidea (family SINENTOMIDAE). Though most workers consider the Eosentomidae and Sinentomidae as the most primitive proturans, their possession of a tracheal system and certain features of their sperm have led Yin (1984) to propose that they are more specialized than the Acerentomoidea.

Literature

Most literature on Protura is taxonomic. Accounts of the biology of this group are given by Ewing (1940), Nosek (1973), and Imidaté (1991). Nosek (1973) provides a key to the European species and Nosek (1978) a key to the world genera; Ewing (1940) deals with the North American forms; and Imidaté (1991) with the Australian families.

Ewing, H. E., 1940, The Protura of North America, *Ann. Entomol. Soc. Am.* **33**:495–551.

Imidaté, G., 1991, Protura, in: *The Insects of Australia*, 2nd ed., Vol. I (CSIRO, ed.), Melbourne University Press, Carlton, Victoria.

Nosek, J., 1973, *The European Protura*, Museum d'histoire naturelle, Geneva.

Nosek, J., 1978, Key and diagnosis of Protura genera of the world, *Annot. Zool. Bot. Bratislava* **122**:1–59.

Tuxen, S. L., 1964, *The Protura. A Revision of the Species of the World with Keys for Determination*, Hermann, Paris.

Yin, W.-Y., 1965, Studies on Chinese Protura. II. A new family of the suborder Eosentomoidea, *Acta Entomol. Sin.* **14**:186–195. (In Chinese with English summary.)

Yin, W.-Y., 1984, A new idea on phylogeny of Protura with approach to its origin and position, *Sci. Sin. (B)* **27**:149–160.

4. Diplura

SYNONYMS: Dicellura, Entotrophi, Entognatha COMMON NAME: diplurans

Elongate apterygotes; head with long many-segmented antennae, compound eyes, and ocelli absent, mouthparts entognathous; thoracic segments distinct, legs with unsegmented tarsus; abdomen 10-segmented, most pregenital segments with styli, eversible vesicles on some abdominal segments, cerci present as either long multiannulate or forcepslike structures, gonopore between segments 8 and 9.

More than 800 species of this widely distributed, though mainly tropical or subtropical, order have been described. Most holarctic forms belong to the family Campodeidae, including the 11 British species. Just over 60 species have been described from North America, and about 30 from Australia.

Structure

In general form Diplura (Figure 5.3) resemble Thysanura but differ in being entognathous and lacking a median process on the last abdominal segment. Most species are a few millimeters long, but a few may reach almost 60 mm. The roundish or oval head carries the multisegmented antennae, whose flagellar segments (except the most distal) are provided with muscles. The reduced biting mouthparts occupy a pouch on the ventral surface. The six identical legs have an unsegmented tarsus. Two to four lateral spiracles occur on the thorax. Ten abdominal segments are distinguishable. The sterna of segments 2–7 bear styli, and eversible vesicles occur on a varied number of segments. The conspicuous cerci vary in structure and are an important taxonomic feature. In most Diplura (but not Campodeidae, which have none) there are seven pairs of abdominal spiracles.

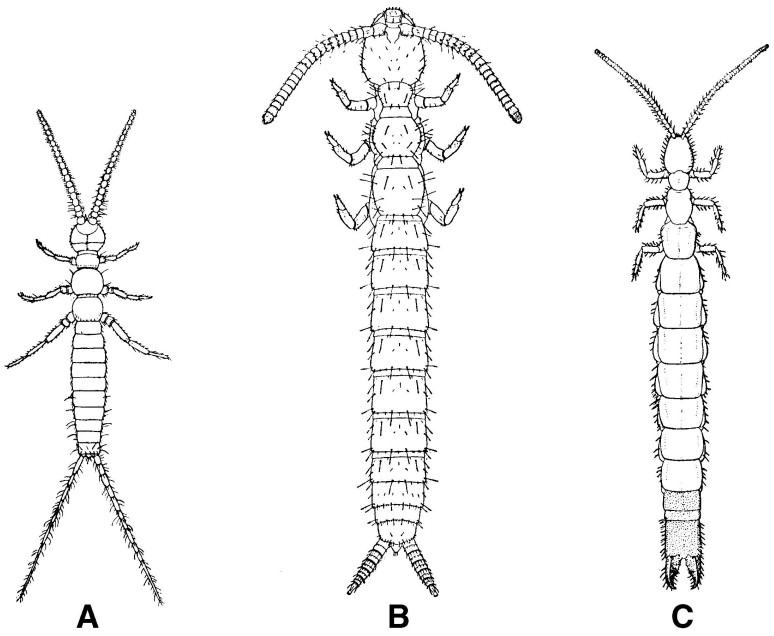

FIGURE 5.3. Diplura. (A) *Campodea* sp. (Campodeidae); (B) *Anajapyx vesiculosus* (Anajapygidae); and (C) *Heterojapyx* sp. (Heterojapygidae). [From A. D. Imms, 1957, *A General Textbook of Entomology*, 9th ed. (revised by O. W. Richards and R. G. Davies), Methuen and Co.]

As in Protura, Malpighian tubules are represented usually by a varied number of papillae at the junction of the midgut and hindgut. The tracheal system is developed to a varied extent. Tracheae leading from one spiracle never anastomose with those from other spiracles, and they lack cuticular supporting rings characteristic of insectan tracheae. The nervous system is not specialized, the ventral nerve cord containing eight (Japygidae) or seven (other Diplura) abdominal ganglia. The reproductive system is greatly varied within the Diplura, although in all species the germaria are apical. In *Japyx* (Japygidae) there are seven pairs of segmentally arranged ovarioles, in *Anajapyx* (Anajapygidae) two, and in *Campodea* (Campodeidae) one. One or two pairs of testes occur in the male.

Life History and Habits

Because of their rather secretive habits little is known of the life history of diplurans. They are found in damp habitats, for example, leaf litter, under stones and logs, and in soil. The campodeids are herbivorous, but other Diplura are carnivorous, catching prey with their forceps (modified cerci) or with their maxillae. Like male springtails, male diplurans deposit stalked spermatophores but make no attempt to attract females to them. The eggs are laid in groups in a chamber dug by the female. In some species the female guards the eggs and young. Development is slow and molting (up to 30 times in *Campodea*) continues through life.

Phylogeny and Classification

Fossil Diplura are known from the Upper Carboniferous of Illinois (*Testajapyx thomasi*) though at this stage the appendages were still fully segmented, eyes were present, and the entognathous condition was not fully developed; that is, the lateral margins of the head were not fused with the labium to form a pouch around the mandibles and maxillae. Extant Diplura were arranged by Paclt (1957) in three families [CAMPODEIDAE, PROJAPYGIDAE (= ANAJAPYGIDAE), and JAPYGIDAE]. However, more recent classifications [e.g., that of Condé and Pagés (1991)] tend to raise the subfamilies within these groups to the rank of family. In campodeids (Figure 5.3A), which may reach 4 mm at maturity, the cerci are multiannulate and usually as long as the abdomen. In contrast, the projapygids (Figure 5.3B) are minute arthropods with relatively short cerci (less than half the length of the abdomen and having fewer than 10 subdivisions). The cerci of japygids (in the sense of Paclt, 1957) take the form of strongly sclerotized, undivided forceps (Figure 5.3C).

Literature

General information on Diplura is given by Wallwork (1970) and Condé and Pagés (1991). Most North American species can be identified from Smith (1960), the British species from Delany (1954), and the Australian families from Condé and Pagés (1991).

Condé, B., and Pagés, J., 1991, Diplura, in: *The Insects of Australia*, 2nd ed., Vol. I (CSIRO, ed.), Melbourne University Press, Carlton, Victoria.

Delany, M. J., 1954, Thysanura and Diplura, *R. Entomol. Soc. Handb. Ident. Br. Insects* **1**(2):1–7.

Paclt, J.,1957, Diplura, *Genera Insect.* **212**:1–123.

Smith, L. M., 1960, The family Projapygidae and Anajapygidae (Diplura) in North America, *Ann. Entomol. Soc. Am.* **53**:575–583.

Wallwork, J. A., 1970, *Ecology of Soil Animals*, McGraw-Hill, New York.

5. Microcoryphia

SYNONYMS: Archeognatha, Ectotrophi (in part), Ectognatha (in part)

COMMON NAME: bristletails

Small or moderately sized apterygote insects; head with long multiannulate antennae, large contiguous compound eyes, ocelli, ectognathous chewing mouthparts, mandibles with single articulation, maxillary palps 7-segmented; thorax strongly arched with terga extending over pleura, legs with 3 (rarely 2) tarsal segments; abdomen 11-segmented, though 10th segment reduced and tergum of 11th forming median caudal filament, paired styli present on each abdominal segment, long cerci with multiple subdivisions present.

As noted in the Introduction to this chapter, Microcoryphia and Zygentoma (see Section 6) were originally united in the order Thysanura. However, fundamental differences in their structure (compare the definitions of the orders) have led to their separation as distinct orders. The Microcoryphia form a small (about 350 species) but cosmopolitan group, with about 35 species in North America (mostly Machilidae), 7 in Australia (all Meinertellidae), and 7 in Britain (all Machilidae).

Structure

Microcoryphia (Figure 5.4A) are elongate insects up to 20 mm in length. Their body is strongly convex dorsally (with the large terga extending around the sides to cover the pleura), generally tapered posteriorly, and covered with scales. The head is hypognathous, in some species prognathous, and carries prominent chewing mouthparts, the long, 7-segmented maxillary palps being particularly conspicuous. Each mandible has a single articulation with the head. The antennae are filiform and comprise 30 or more subdivisions that lack intrinsic musculature. Compound eyes are well developed and contiguous (meet in a middorsal position). Median and paired lateral ocelli are also present. The legs have three tarsal segments and, in some species, those of the mesothorax and metathorax bear coxal styli. Abdominal styli occur on segments 2–9, and eversible vesicles are almost always found on abdominal segments 1–7. In females an ovipositor is formed from the appendages of

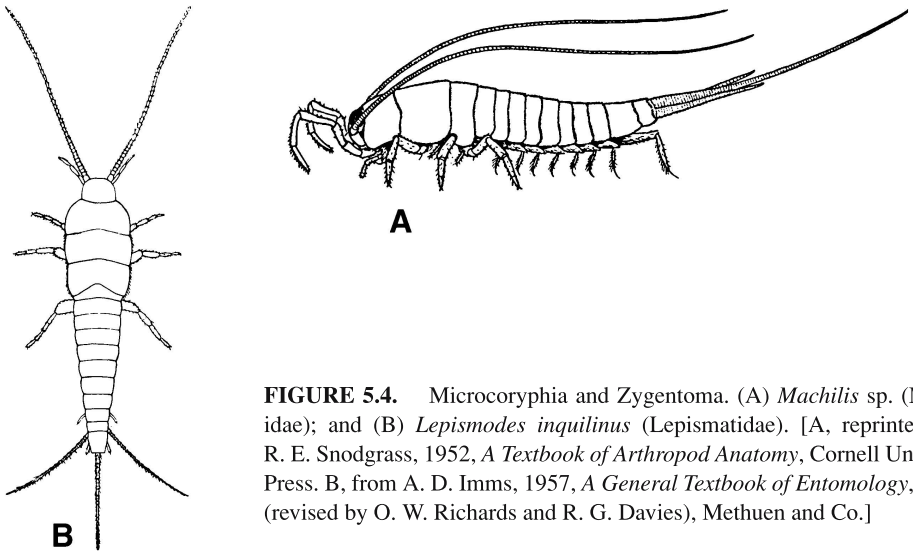

FIGURE 5.4. Microcoryphia and Zygentoma. (A) *Machilis* sp. (Machilidae); and (B) *Lepismodes inquilinus* (Lepismatidae). [A, reprinted from R. E. Snodgrass, 1952, *A Textbook of Arthropod Anatomy*, Cornell University Press. B, from A. D. Imms, 1957, *A General Textbook of Entomology*, 9th ed. (revised by O. W. Richards and R. G. Davies), Methuen and Co.]

abdominal segments 8 and 9. In males the appendages of the ninth abdominal segment fuse to form a median penis.

Internally Microcoryphia exhibit features that might be expected of primitive insects. They have 12–20 Malpighian tubules, a nervous system that includes paired longitudinal connectives, 3 thoracic and 8 abdominal ganglia, 9 pairs of spiracles and tracheae that do not anastomose with those of adjacent segments, and a primitive reproductive system. In females there are typically seven or eight panoistic ovarioles on each side of the body, and in some species these are arranged in a more or less segmental manner. Females lack a spermatheca. In males each testis comprises three or four follicles, and the vas deferens on each side is double, the two channels being connected by several transverse tubes.

Life History and Habits

Microcoryphia are usually nocturnal, hiding by day in rotting wood, among leaves, in crevices, under stones, etc., and are restricted to such habitats by their inability to resist desiccation. They are phytophagous or omnivorous, feeding on algae, lichens, leaf litter, and sometimes other arthropods. Bristletails can run fairly quickly and sometimes jump (up to 10 cm).

Details of the life history of Microcoryphia are not well known. Though parthenogenesis occurs in some species, reproduction is usually sexual, males leaving stalked spermatophores on the substrate or placing a sperm droplet on the ovipositor. Females lay eggs singly or in batches of up to 30 in crevices or holes dug with the ovipositor. The absence of a spermatheca suggests that mating must occur frequently. Postembryonic development is slow (generally taking several months to a year from hatching to adulthood) and includes at least five juvenile instars in *Machilis.* Molting continues in adults.

Phylogeny and Classification

Fossil machilids are known from as early as the Lower Devonian of Quebec. Extant species are placed in the single superfamily Machiloidea, containing two families, the MACHILIDAE and the more primitive MEINERTELLIDAE. The former is principally a Northern Hemisphere group while the latter is mainly from the Southern Hemisphere.

Literature

See under Section 6 (Zygentoma).

6. Zygentoma

SYNONYMS: Thysanura (*sensu stricto*),
Ectotrophi (in part),
Ectognatha (in part)

COMMON NAME: silverfish, firebrats

Small or moderately sized, dorsoventrally flattened apterygote insects; head with long multiannulate antennae, compound eyes small or absent, ocelli absent (except Lepidotrichidae), ectognathous chewing mouthparts, mandible with dicondylic articulation, maxillary palp 5-segmented; legs with 2–4 tarsal segments; abdomen 11-segmented but with 10th segment

reduced and tergum of 11th segment forming median caudal filament, paired styli on abdominal segments 7–9 (rarely 2–9), cerci generally long with multiple subdivisions, but sometimes quite short, strongly diverging from body.

The Zygentoma is a small, worldwide order of about 370 species that are both structurally and ecologically more diverse than microcoryphians. About 30 species have been described from North America, with about the same number from Australia, including some that are cosmopolitan and occasionally pests, and 2 from Britain (both Lepismatidae).

Structure

Zygentoma (Figure 5.4B) are broadly similar to Microcoryphia, and only the more important differences in structure will be noted here. The body of Zygentoma is dorsoventrally flattened and may or may not have scales. Compound eyes are reduced or absent and ocelli do not occur (except in Lepidotrichidae). The maxillary palps are 5-segmented, and the mandibles have a dicondylic articulation with the head, as do those of pterygote insects. The legs include 2–4 tarsal segments. Abdominal styli normally occur only on segments 7–9, though in Nicoletiidae they are found on segments 2–9. Eversible vesicles are absent in many Lepismatidae but occur on abdominal segments 2–7 in Nicoletiidae and Lepidotrichidae. In most species the cerci are long, multiannulate structures that diverge sharply from the body (Figure 5.4B). However, in some inquiline Nicoletiidae the cerci are very short.

Four to eight Malpighian tubules are present. Ten pairs of spiracles occur and the tracheal system is well developed compared to that of Microcoryphia. On each side of the body a longitudinal trunk links the tracheae originating from the spiracles, and transverse segmental tracheae unite one side with the other. The female reproductive system includes 2–7 panoistic ovarioles, a spermatheca, and accessory glands. The number of lobes comprising each testis is greater than in Microcoryphia (eight lobes in Lepismatidae, many in Nicoletiidae and Lepidotrichidae).

Life History and Habits

Though many Zygentoma resemble Microcoryphia in their general habits, living in leaf litter, under bark, and in other places with high humidity, others are extremely resistant to desiccation and have the ability to take up water from the atmosphere. All are very agile insects. Zygentoma are omnivorous or phytophagous.

Eggs are laid singly or in groups, in crevices, etc. Individuals may live for several years, and as many as 60 molts have been recorded. About a dozen molts occur before sexual maturity is reached. Because the lining of the spermatheca is shed at each molt, females must mate between molts in order to produce fertilized eggs. The majority of species reproduce sexually, males producing stalked spermatophores that are deposited on the substrate for females to pick up as in Microcoryphia. However, parthenogenesis probably occurs in a few species where males are very scarce.

Phylogeny and Classification

The earliest known fossil zygentoman is *Ramsdelepidion schusteri* from the Upper Carboniferous of Illinois. This was a large (6 cm long) insect with such primitive features as a full set of long, abdominal, fully segmented leglets, and two pairs of vesicles on the ventral

side of abdominal segments 1–7. Extant species fall into four families (LEPISMATIDAE, NICOLETIIDAE, LEPIDOTRICHIDAE, and MAINDRONIIDAE), of which only the first two are of any size. Though most Lepismatidae live in litter, under bark, etc., the family includes a number of domiciliary species (found in buildings) that have been transported worldwide by human activity, including the common silverfish, *Lepismodes inquilinus,* and the firebrat, *Thermobia domestica.* The former prefers warm and humid environments and is often found in places such as bookcases, cupboards, and bathrooms. Firebrats, in contrast, live in hot, dry environments, for example, in the vicinity of fireplaces, furnaces and boilers, and in bakeries. They are highly resistant to desiccation. Both species may cause considerable damage to books, clothing, and foods that contain starch or cellulose, and they are among the few animals that produce an intrinsic gut cellulase. The Nicoletiidae, which are distinguished from Lepismatidae by not having compound eyes, live principally in caves or underground though some are inquilines in the nests of ants and termites, stealing the hosts' food or causing the host to regurgitate fluids on which they feed.

The Lepidotrichidae should be mentioned in view of this family's important phylogenetic position. Prior to 1961 the family was known only as fossils. However, in 1961 Wygodzinsky discovered a living representative, *Tricholepidion gertschi*, in California, that possesses a large number of primitive characters. This species is clearly the most archaic living apterygote insect discovered to date and is likely to be similar to the common ancestor of other modern groups.

Literature

Accounts of the biology of Microcoryphia and Zygentoma are provided by Delaney (1957) and Sharov (1966). Keys for identification are given in the papers by Delany (1954) [British species], Wygodzinsky (1972) [North and Central American Lepismatidae], and Wygodzinsky and Schmidt (1980) [Microcoryphia of eastern North America].

Delany, M. J., 1954, Thysanura and Diplura, *R. Entomol. Soc. Handb. Ident. Br. Insects* **1**(2):1–7.

Delany, M. J., 1957, Life histories in the Thysanura, *Acta Zool. Cracov.* **2**:61–90.

Sharov, A. G., 1966, *Basic Arthropodan Stock*, Pergamon Press, Elmsford, NY.

Wygodzinsky, P., 1961, On a surviving representative of the Lepidotrichidae (Thysanura), *Ann. Entomol. Soc. Am.* **54**:621–627.

Wygodzinsky, P., 1972, A review of the silverfish (Lepismatidae, Thysanura) of the United States and the Caribbean Area, *Am. Mus. Novit.* **2481**:26.

Wygodzinsky, P., and Schmidt, K., 1980, Survey of the Microcoryphia (Insecta) of the northeastern United States and adjacent provinces of Canada, *Am. Mus. Novit.* **2701**:17.